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Research Article

Invasion impact of two goldenrods (*Solidago canadensis* and *S. gigantea*) on species diversity of plant guilds and soil environment

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Abstract

Two perennial goldenrods, *Solidago canadensis* and *S. gigantea* (Asteraceae), are considered successful plant invaders with an exceptional ability to affect the biodiversity and environment of native ecosystems in Europe. However, their species-specific invasion impacts and associated ecological mechanisms shaping the species diversity of plant guilds and the soil conditions in grasslands remain poorly understood. Here, a spatial invasion-gradient approach with different invasion levels categorised by the percentage of goldenrod cover (heavily invaded > 50%, transitional invaded 20–50% and uninvaded control plots) was used to assess invasion impacts on species diversity of forbs, graminoids and bryophytes as well as on soil and vegetation properties in semi-natural grasslands of Slovakia (Central Europe). Multi-guild diversity assessment showed that graminoids were more tolerant than forbs of the competitive and stressful conditions in invaded plots. Invasion level reduced species richness of forbs in heavily invaded plots, likely owing to intensified competition and litter accumulation generated by dense *Solidago* stands. No invasion effect was found on graminoid and bryophyte species diversity metrics. Most variation in species diversity and ecological responses was addressed to the shared invasion impacts of both *Solidago* species, but several species-specific invasion effects on forb diversity indices and soil chemistry (soil reaction, nitrogen and potassium concentrations, C-to-N ratio) were also identified. The contrasting forb responses in Shannon and Simpson diversity indices corresponded to shifts in community evenness associated with species-specific effects of the invaders on soil nutrient cycling and productivity. Goldenrod invasions also altered community structure, primarily through shifts in abundance-dominance interactions rather than through substantial species replacement. Our results highlight the importance of recording invasion impacts across functional guilds and ecosystem components to better understand the mechanisms of plant invasion in semi-natural grasslands.

Key words: Bryophytes, competitive exclusion, diversity indices, forbs, graminoids, litter accumulation, semi-natural grasslands, soil chemistry

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Introduction

Biological invasions pose an urgent challenge to community ecology because their detrimental effects on ecological processes operate at different spatial and biological levels – from species to ecosystems (Vilà et al. 2011; Lopez et al. 2022). Their impact consists of a series of changes in biotic interactions (Mitchell et al. 2006),

biogeochemical (nutrient) cycles (Dassonville et al. 2008; Liao et al. 2008) and habitat structure (Vilà et al. 2006). Understanding the magnitude of invasion impacts on natural systems is important from both a theoretical and practical perspective, as invasion processes often imply loss, or at least degradation, of the ecological and conservation value of resident ecosystems (Pyšek et al. 2020).

Plants vary in life and reproduction strategies and functional traits (i.e. in the breadth of species' niches) that shape species-specific eco-physiological performance, including the ability to colonise new sites. Some plant species exceed the limits of their natural geographic range due to human events and become naturalised or invasive aliens in novel regions (Weber and Jakobs 2005). The invasive plants frequently achieve a high relative abundance in the plant community. These local dominants play a crucial role in community organization, as they drive the competitive hierarchy and the degree of biotic interactions among individuals (Mitchell et al. 2006). The competitive superiority of dominant plant species strongly influences the fine-scale partitioning of above- and belowground resources and the availability of these resources to less-abundant (subordinate) species (Gioria and Osborne 2014). Successful plant invaders may thus threaten biodiversity and ecosystem functioning (Daru et al. 2021), which has been manifested at multiple scales (Parker et al. 1999).

Intensive biodiversity research suggested correlations between the high abundance, density and/or biomass of invasive alien species and the loss of native plant diversity in recipient ecosystems (e.g. Vilà et al. 2011; Pyšek et al. 2020), leading to homogenisation of species composition (Daru et al. 2021). However, this species-reducing impact may be confounded by the more complex interactive effects of predictors (Didham et al. 2007) and by the environmental settings of pre-invaded communities (Funk and Vitousek 2007; Goossens et al. 2024). Accordingly, positive (Pyšek et al. 2012; Lefebvre et al. 2024), negligible (Diekmann et al. 2016; Čuda et al. 2017) or no (neutral) effects (e.g. Scharfy et al. 2009) of invasive alien species on the species diversity and/or ecology of native communities have also been identified. Similarly, a meta-analysis assessing the environmental impact of plant invasions yielded context-dependent results (Pyšek et al. 2012), with no consensus on how alien populations affect the soil resources (Ehrenfeld 2003). For example, although soil nutrient concentrations in invaded ecosystems are generally driven by soil productivity gradients (Sardans et al. 2017), the dominance of plant invaders can alter soil pools of limiting nutrients, mainly nitrogen (Liao et al. 2008) and phosphorus (Zhang et al. 2009a). The high stock of these mineral nutrients in soil and their availability to plants may facilitate plant invasion success (Vilà et al. 2011), but plant invaders are also able to spread in less-fertile soils (Goossens et al. 2024). Divergent results tend to follow the whole study context, including species-specific functional traits, geographical and temporal scales as well as environmental circumstances (Dassonville et al. 2008; Vilà et al. 2011; Bartz and Kowarik 2019).

Two tall perennial herbaceous species, *Solidago canadensis* L. and *S. gigantea* Ait. (Asteraceae), native to North America, are exceptionally successful invaders in Europe (Weber 1998; Weber and Jakobs 2005; Szymura and Szymura 2015). They effectively grow, reproduce and spread in various sites and habitats, but their ecological niches and habitat preferences differ. While *S. canadensis* thrives in a variety of human-made habitats and mesic grasslands in hilly regions of Central Europe, *S. gigantea* prefers rather flat and low-altitudinal floodplains along rivers or forest clearings and plantations (Skokanová et al. 2024; but see Perera et al. 2021). Both invasive goldenrod (*Solidago*) species share some habitat types,

including unmanaged, low-intensity or irregularly managed roadsides and grasslands (Skokanová et al. 2024). Importantly, both goldenrods differ in their life history traits, most notably in biomass allocation strategy. Specifically, *S. canadensis* allocates a large proportion of its biomass to aboveground organs and produces numerous seeds through its flowering shoots. In contrast, *S. gigantea* invests more resources in belowground biomass and clonal growth via long, branched rhizomes (Schmid et al. 1988; Szymura and Szymura 2015; Skokanová 2023).

Previous research has usually focused on the invasion impacts of a single *Solidago* species (de Groot et al. 2007; Scharfy et al. 2009; Bielecka et al. 2020; Xie et al. 2022; Goossens et al. 2024), or compared it with invasive representatives of other genera (Dassonville et al. 2008; Stefanowicz et al. 2017). Moreover, few studies have disentangled the impact of invasive *Solidago* species on diversity patterns using a multi-guild assessment (e.g. forbs and graminoids; Grange et al. 2023), even though this approach presents a novel research perspective and provides a more detailed insight into the main components of plant communities. Lower values of total plant diversity on sites invaded by *S. canadensis* compared to uninvaded plots have mostly been reported in the scientific literature (e.g. de Groot et al. 2007; Wang et al. 2018; Xie et al. 2022), but several case studies have also shown opposite results (e.g. Dong et al. 2015). This species was found to restrain the richness of annual and perennial plants in urban areas (Bielecka et al. 2020), but its effect on the diversity of plant guilds prevailing in other habitats (e.g. in grasslands) remains less understood. It reduces diversity values either directly due to high biomass production (see biomass allocation strategies; Ren et al. 2019) or indirectly through species-induced changes in the soil environment and biota (Abhilasha et al. 2008; Zhang et al. 2009a). Plant-soil interactions suggest that *S. canadensis* decreases total soil nitrogen and phosphorus content (Zhang et al. 2009a), but increases soil organic carbon, C-to-N ratio (Bielecka et al. 2020), soil pH and bulk density (Zhang et al. 2009a). In addition, allelopathic compounds produced by this species are another important source of changes in soil quality and interspecific interactions. In this case, allelopathy diminishes populations of native species (Abhilasha et al. 2008; Yuan et al. 2013), with a stronger inhibition effect observed on forb than on graminoid species (Grange et al. 2023). This phytotoxic or at least fitness-reducing effect may be accompanied by an additional suppression of soil pathogen activities, which could enhance the growth and vitality of *S. canadensis* (Zhang et al. 2009b). Based on this evidence, this perennial herb species was listed among the species with the greatest environmental impact in Europe (Rumlerová et al. 2016).

The invasive species *S. gigantea* is also acknowledged to have significant impacts on belowground processes. It significantly contributes to nutrient turnover rates in invaded communities (Chapuis-Lardy et al. 2006; Vanderhoeven et al. 2006). This species benefits from mycorrhizal relationships and the ability to acidify topsoil layers, resulting in modification of the storage, fluxes and concentrations of plant-available phosphorus (Chapuis-Lardy et al. 2006; Herr et al. 2007). Previous research has reported an increase in soil fungal biomass (Scharfy et al. 2010) and aboveground herb biomass in invaded plots (Vanderhoeven et al. 2006; Scharfy et al. 2009), which coincides with a decrease in plant diversity of the invaded vegetation (e.g. Pal et al. 2015; Stefanowicz et al. 2017). The species invasion effect on some soil parameters (e.g. soil reaction, nitrogen dynamics) appears to yield equivocal results, likely due to differences in soil fertility on pre-invaded plots (Vanderhoeven et al. 2006; Funk and Vitousek 2007).

In this study, we assessed variation in plant diversity associated with the presence of two invasive species *S. canadensis* and *S. gigantea* in semi-natural grasslands, because – i) both species differ in their life history traits (Schmid et al. 1988; Szymura and Szymura 2015), realised niches and ecological preferences (Skokanová et al. 2024); ii) a disproportionately large number of empirical studies focused on *S. canadensis* than on *S. gigantea* (Regulska et al. 2026), which yielded conflicting invasion impacts on ecosystem components; iii) ongoing climate change is expected to further accelerate the spread of both species in the eastern part of Central Europe (Skokanová et al. 2024); and iv) grassland habitats are generally subjected to large-scale land-use changes (Auffret et al. 2018), which can lead to the degradation of their species composition (Hegedüšová Vantarová and Škodová 2014) and increase the risk of invasion. We were also particularly interested in assessing the impact of invasions on soil properties, as these can reflect changes in ecosystem processes (Vilà et al. 2006). Specifically, we aimed to address the following questions: (1) Does invasion by the perennial goldenrods *S. canadensis* and *S. gigantea* shape the species diversity of plant guilds (forbs, graminoids and ground-dwelling bryophytes) in semi-natural grasslands? (2) Do these invasive goldenrod species cause changes in soil chemistry and vegetation characteristics? and (3) Does invasion affect the species composition of resident (native) plant communities? We hypothesised that both invasive plant species analysed would reduce species diversity measures (hypothesis 1) and that modifications in soil fertility factors would mirror invasion impact (hypothesis 2). To test our hypotheses, we employed a spatial invasion-gradient approach using a comparative design of invaded plots with adjacent and environmentally similar uninvaded plots, assuming that the latter represented the pre-invasion situation.

Materials and methods

Study sites and sampling design

The invasion effect of *Solidago canadensis* and *S. gigantea* on the resident vegetation and environment was studied at 20 sampling sites (10 sites per species) distributed across western, southern and central Slovakia during the summer of 2021 (Fig. 1). The mean annual temperature and precipitation of the recorded sites were 8.8 °C (7.9–10.1/min.–max.) and 600 mm (560–684/min.–max.), respectively (period 1991–2020; Slovak Hydrometeorological Institute, Bratislava).

Sampling sites comprised various grassland communities ranging from open dry grasslands on sandy soils to mesic grasslands. They were selected based on the current distribution of *Solidago* species in the area and reflecting the partially contrasting habitat preferences of both species (Skokanová et al. 2024). Sampling sites included well-established and self-reproducing populations with diploids of *S. canadensis* and tetraploids of *S. gigantea* (Skokanová et al. 2025) that had been present at the sites for at least five years. Mixed populations were not sampled. The selected sites were either abandoned or only occasionally managed, but they had not been mown in the vegetation season of 2021. We did not sample sites with shrubs and trees present. The invaded vegetation patches were surrounded by semi-natural grasslands, which corresponded to EUNIS (European Nature Information System) habitats of R22 – Low and medium altitude hay meadow, occasionally to R1B – Continental dry grassland, and R1P – Oceanic to subcontinental inland sand grassland on dry acidic and neutral soils. At each sampling site, we set

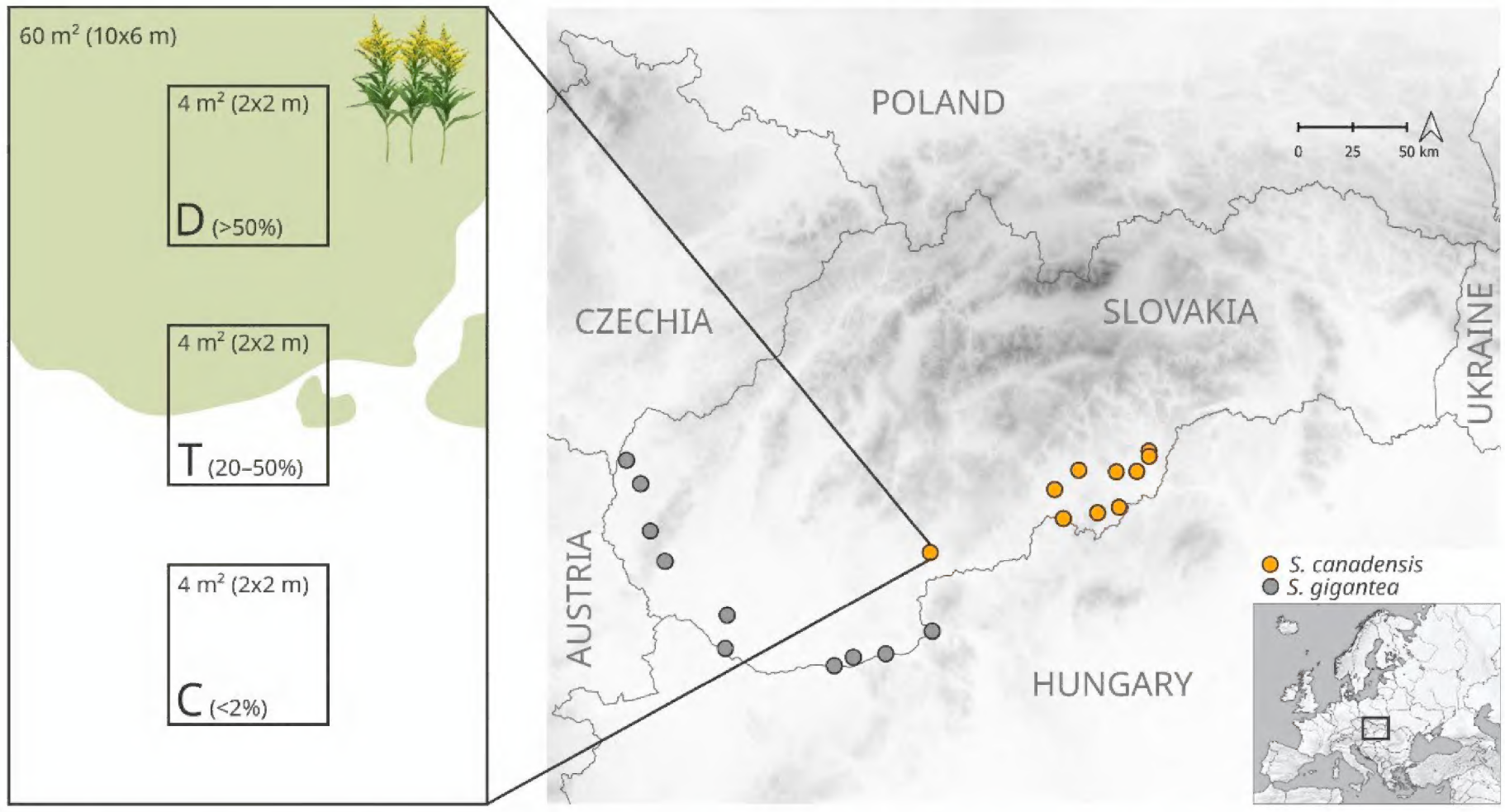

Figure 1. Distribution of sampling sites for invasive species *Solidago canadensis* (orange dots; n = 10) and *S. gigantea* (grey dots; n = 10) in Slovakia (Central Europe). Three square sampling plots (2 × 2 m) with different percentage cover of the target invasive species were established at each site (C – uninvaded control plot; T – transitional plot with goldenrod cover in the range of 20–50%; D – heavily invaded plot with dominant cover of *S. canadensis* or *S. gigantea* > 50%). These triplet plots were embedded in a large rectangular plot. Green patches on the left side correspond to the population of *Solidago* species at each study site.

up three square permanent plots (2 × 2 m) categorised by the percentage cover of the target invasive species (referred to as invasion level), namely heavily invaded (dominant cover of *S. canadensis* or *S. gigantea* > 50%, labelled as D), transitional (20–50%, T) and uninvaded control (C) plots. In a few cases, the control plot contained one or two *Solidago* individuals (sterile or juvenile plants), but their cover values never exceeded 2% cover (invasion impact, mean ± SD) for S. *canadensis* (C – 0.04 ± 0.10%; T – 25.0 ± 3.6%; D – 71.9 ± 13.6%) and *S. gigantea* (C – 0.35 ± 0.67%; T – 27.9 ± 4.2%; D – 84.2 ± 13.0%). Invaded and control plots were located as close as possible to each other (but with buffer space of at least 0.5 m width) in a direct line and were embedded in a 60 m² rectangular plot with dimensions of 6 × 10 m or 5 × 12 m (less frequently of 4 × 15 m; Fig. 1). Established plots within the sampling site had similar topographic positions and the same management treatment in order to minimise the confounding effects of site ecology and management events on invasion effect (Dassonville et al. 2008). This spatial invasion-gradient approach allowed us to interpret all potential differences between plots in terms of invasion impact.

Field sampling and laboratory analyses

We recorded percentage cover for all vascular plants and ground-dwelling bryophytes in each sampling plot (Suppl. material 1: table S1). To explore the invasion impact of *Solidago* species on environment and vegetation properties, recording of plant community characteristics and soil sampling was performed at each plot (Suppl. material 1: table S2). We visually estimated the percentage cover of the moss-layer, organic litter and bare soil. For each plot, litter thickness and soil depth (using a metal rod of 1 cm in diameter) were measured at five points (i.e. central

points of the plot and each plot quadrat), and their mean values were used for analyses. Slope inclination was measured with a clinometer. Geographical coordinates of plot corners were measured using an Emlid Reach RS2+ GNSS receiver (Emlid, Hungary) with submeter accuracy (usually several centimetres) and collected through the Emlid Flow application.

Five soil samples were collected from a topsoil mineral horizon (0–10 cm) along the diagonal of each plot and homogenised to form one composite sample per plot. The surface organic layer was removed before sampling. Soil samples were air-dried at laboratory temperature, gently crushed, and sieved through a 2 mm mesh. They were used to determine basic physical and chemical characteristics. Soil pH was measured potentiometrically in a suspension of 1:2.5 soil/distilled water after 24 h using a pH meter equipped with a pH electrode. Total contents of carbon (C), nitrogen (N) and sulphur (S) were measured using a VarioMacro Elemental Analyzer (CNS Version, Elementar GmbH, Langenselbold, Germany) with the dry combustion method. To determine the organic carbon concentration (C_{org}), carbonate content was measured by volumetric device and after that inorganic carbon content was subtracted from the total carbon concentration. Content of C_{org} and N_{tot} was also used to calculate the C/N ratio. The concentrations of plant-available nutrients (Ca, Mg, K, Na, P) were extracted in Mehlich II solution and measured by inductively coupled plasma optical emission spectrometry (ICP–AES). The proportion of sand, silt and clay fraction in samples was determined using the sedimentation analysis (pipette method).

Response and explanatory variables

Vegetation diversity was estimated using three response variables: Hill–species richness, Hill–Shannon diversity, and Hill–Simpson diversity (Hill 1973; Roswell et al. 2021). They were separately calculated for three plant guilds (forbs, graminoids, bryophytes) and for the herb layer (i.e. forbs and graminoids counted together). Horsetails, seedlings and juveniles of woody species were excluded from analyses. We calculated sample Hill diversities, i.e. so-called Hill numbers of order q = 0 (species richness), q = 1 (Hill–Shannon diversity) and q = 2 (Hill–Simpson diversity) using relative cover data (i.e. cover-abundance) of plant species. The target invasive *Solidago* species were excluded from estimates of forb species richness and diversity, and the remaining forb covers were re-scaled accordingly, as the occurrence and relative cover-abundance of *S. canadensis* and *S. gigantea* were predetermined by the sampling design. Preliminary insights into diversity patterns of the herb layer (Hill–Shannon and Hill–Simpson indices) were calculated with *Solidago* species (e.g. Flory and Clay 2010; Diekmann et al. 2016). To check for the bias due to low sampling coverage (Roswell et al. 2021), sample completeness (the ratio of observed to the true species richness) was assessed for all plots (n = 60) and separately for both *Solidago* species (30 plots each). The sample coverage for both species was over 90.0%. The curves showed similar shapes without any crossing (Suppl. material 1: fig. S1), indicating comparable species richness estimates for *S. canadensis* and *S. gigantea* plots.

In addition to diversity measures, the other plant community characteristics used as response variables were litter thickness and cover of litter, bare soil, moss-layer, and soil chemical parameters (pH, content of C_{org}, N, C/N ratio, S and plant-available Mg, Ca, K, P and Na; Suppl. material 1: table S2). We also used the cumulative cover of herb-layer, forb and graminoid species (defined as the

sum of species percentage covers that can exceed 100%). These variables were used instead of simple total cover, which has a fixed upper limit of 100%, because the latter can potentially underestimate dense, diverse and well-structured vegetation (Axmanová et al. 2012). Cumulative herb-layer cover, including *Solidago* species, was used as a proxy for standing vegetation biomass shaping the intensity of competitive interactions (Goldberg 1987; Axmanová et al. 2012).

Explanatory variables included *Solidago* species (as a categorical variable with two levels, i.e. *S. canadensis* and *S. gigantea*), invasion level (ordinal variable with three levels) and their interaction. The list of explanatory variables was also enriched by slope, soil clay content and soil depth (continuous variables), as vegetation plots invaded by *S. gigantea* were more common on flat slopes (1.7 ± 2.4°; mean ± SD) with sandy (54.4 ± 27.1%) and shallower (29.5 ± 17.8 cm) soils compared to *S. canadensis* (12.6 ± 6.9°, 27.6 ± 17.62%, 39.4 ± 13.2 cm; Suppl. material 1: table S2). Clay content was used in all models because soil texture parameters (sand, silt and clay) are compositional fractions summing to 100% (i.e. they are not statistically independent). Scaled continuous explanatory variables were used in all models.

Data analyses

The Pearson correlation between continuous variables and point-biserial (Pearson) correlation between *Solidago* species and continuous explanatory variables was computed to assess association between variables (Suppl. material 1: tables S3–S5). To avoid pseudoreplication due to multiple plots per locality, correlation analyses were restricted to control (C) plots only. Generalized linear mixed-effect models (GLMMs) and linear mixed-effect models (LMMs) were employed to analyse invasion impacts of the *Solidago* species (and their interactions with invasion levels) and the potential effects of other explanatory variables (soil clay, soil depth, slope) on plant diversity measures, vegetation and soil properties. Sampling site (locality) was implemented as a random effect to account for the spatial non-independence of plots within each sampling site. The interaction between continuous explanatory variables and invasion level was not included in the models to keep models parsimonious. GLMMs were fitted using a Poisson distribution with a log link for species richness (COM-Poisson for graminoid richness), a Gamma distribution with a log link for cumulative covers of herb-layer, forb, and graminoid species (because dispersion differed among plot types for graminoids, we fitted a Gamma GLMM with a plot-specific dispersion structure), and a Beta distribution with a logit link for litter, moss-layer and bare ground covers. The latter two were adjusted following the Smithson–Verkuilen transformation ($(y \times (n - 1) + 0.5) / n$) prior to analysis to avoid boundary values (i.e. zeros). LMMs were used for soil pH, other soil chemical parameters, and Hill–Shannon and Hill–Simpson diversity indices. These variables were log-transformed where appropriate (moss values: $y + 0.0001$ prior to transformation). Analysis-of-variance tables (type II Wald χ^2 tests) were calculated for GLMM and LMM models, and model assumptions were checked using standard diagnostic procedures. For herb-layer cumulative cover, clay content was modelled using a second-order polynomial term to improve model fit and diagnostic. Post-hoc inference was based on estimated marginal means (EMMs) derived from fitted (G)LMMs. When the '*Solidago* × Invasion level' interaction effect was significant ($P < 0.05$), it was decomposed using planned contrasts. These included within-species comparisons of invasion levels (D vs. C) and a contrast-in-contrast

test comparing the magnitude of the invasion effect (D–C) between species. These contrasts were defined a priori to test specific ecological hypotheses and to limit multiple testing. When the interaction effect was not significant, the main effects of *Solidago* species identity and/or invasion level were interpreted. Pairwise comparisons among factor levels were conducted using Tukey-adjusted contrasts. Compact letter displays were used only for these main-effect comparisons. All post-hoc tests were performed on the model (link) scale with appropriate multiplicity adjustment. Results are presented as back-transformed estimated marginal means with 95% confidence intervals. Nakagawa's pseudo-R^2 for the analysed models was calculated, with the marginal R^2 (the variance explained by fixed factors), and the conditional R^2 (the variance explained by fixed and random factors). We additionally applied a plot-based rarefaction-extrapolation approach based on incidence data (including the *Solidago* spp.) to describe patterns of species accumulation with increasing numbers of plots and to compare richness between invasion levels separately for *S. canadensis* and *S. gigantea*. These analyses were treated as descriptive and supplementary to the mixed-effects models because plots were nested within sites and were therefore not independent random samples.

Effects of invasive *Solidago* species, invasion levels and environmental variables (soil clay content, slope, soil depth) on plant species composition of semi-natural grasslands were tested by permutational multivariate analysis of variance (PERMANOVA; Anderson 2001), using the Bray-Curtis dissimilarities calculated from species cover data and with 999 permutations stratified within locality. Prior to multivariate analyses, the species data matrix was modified by removing i) both invasive *Solidago* species, and ii) species occurring in less than three plots in order to reduce noise and avoid distortion of distance measures. Preliminary models showed no significant '*Solidago* × Invasion level' interaction effects on species composition ($P > 0.9$). Subsequent analyses were therefore conducted using an additive model to improve parsimony and interpretability. Sequential and marginal tests were compared, with final inference based on marginal (Type III-like) tests. Homogeneity of multivariate dispersion among invasion levels was assessed using betadisper with restricted permutations to evaluate whether significant PERMANOVA results reflected centroid shifts or dispersion differences. Variation in species composition was visualized using non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarities. The two-dimensional and three-dimensional models were performed using the same species compositional matrix to ensure consistency between statistical testing and visualization. Indicator species analysis (IndVal; De Cáceres and Legendre 2009) was conducted to compare species performance and to identify species affinity to invasion levels. The analysis used the IndVal statistic with 999 permutations and the same filtered species matrix as used for PERMANOVA, but with non-transformed cover values. Permutations were restricted within locality to account for spatial structure. Significance (P) levels were adjusted for multiple testing using the Benjamini–Hochberg false discovery rate (FDR) procedure.

All analyses were conducted in R language (ver. 4.5.0, R Core Team 2025) using the 'vegan' (Oksanen et al. 2022), 'iNEXT' (Hsieh et al. 2016, 2022), 'glmmTMB' (Brooks et al. 2017; McGillycuddy et al. 2025), 'lme4' (Bates et al. 2015), 'car' (Fox and Weisberg 2019), 'dplyr' (Wickham et al. 2023), 'multcomp' (Hothorn et al. 2008), 'permute' (Simpson 2022), 'indicspecies' (De Cáceres and Legendre 2009), 'DHARMa' (Hartig 2022), 'performance' (Lüdecke et al. 2021), 'emmeans' (Lenth 2023), 'ggplot2' (Wickham 2016) and 'ggeffects' (Lüdecke 2018) packages.

Results

Environment and vegetation properties

The highest cumulative cover of herb-layer species, including *Solidago*, in heavily invaded plots contrasted with the decline of cumulative cover of forb, excluding *Solidago*, and graminoid species, as well as moss-layer cover, with increasing invasion level (Fig. 2). The effects of invasion level and species identity on litter thickness were statistically significant (Table 1). However, post-hoc comparisons detected differences only between *Solidago* species, with greater litter thickness at sites invaded by *S. canadensis* than by *S. gigantea*. For bare soil cover, the interaction between *Solidago* species and invasion level was significant ($\chi^2 = 6.042$, $P = 0.049$). Post hoc contrasts indicated a decrease in bare soil cover with increasing invasion level in plots invaded by *S. gigantea*, whereas no significant change was found in *S. canadensis* plots. Invasion level had a significant effect on soil Ca and Mg concentrations, but Tukey-adjusted pairwise contrasts did not reveal significant differences among invasion levels (Fig. 2). A significant interaction between *Solidago* species and invasion level was determined for soil pH, K, N, C/N ratio, and S, indicating that invasion effects differed between *S. canadensis* and *S. gigantea*. Soil pH values were lower in heavily invaded plots than in control plots at *S. gigantea* sites, whereas no differences among invasion levels were found for *S. canadensis*; accordingly, the relative invasion effect (D–C contrast) differed significantly between species (RR(D/C): $P = 0.023$). A similar species-specific pattern was observed for soil N, which increased towards plots heavily invaded by *S. gigantea* but showed no differences across invasion levels in plots dominated by *S. canadensis* ($P > 0.05$). Consistently, the relative invasion effect (D–C contrast) differed significantly between both goldenrods (RR(D/C): $P = 0.005$). The significant interaction effect on soil K and C/N ratio (Table 1) reflected species-specific invasion responses despite the absence of significant pairwise differences within species. Post-hoc contrast did not find differences in invasion level between *Solidago* species ($P = 0.150$), although the interaction effect was significant in LMM. All models explained between 2–66% (marginal R^2) of the variance in the environment and vegetation properties, while the inclusion of random effects increased the explained variance to 49–99% (conditional R^2, Table 1).

Species diversity

Three metrics of species diversity – species richness, Hill–Shannon and Hill–Simpson indices – for the three plant guilds showed considerable variance among plots of invasion level. Species richness range was 3–42 for forbs, 3–11 for graminoids and 0–11 for bryophytes per plot (Suppl. material 1: table S2). The most frequent plant taxa recorded in at least 50% of control plots were *Achillea millefolium* agg., *Agrimonia eupatoria*, *Daucus carota*, *Galium verum*, *Lotus corniculatus*, *Picris hieracioides*, *Stenactis annua* (all forbs), *Arrhenatherum elatius*, *Dactylis glomerata*, *Festuca rupicola* (all graminoids) and *Oxyrrhynchium hians* (bryophyte; Suppl. material 1: table S7). The invasion level strongly reduced all species diversity metrics of the herb layer. Diversity values consistently declined in heavily invaded plots, whereas no significant differences were observed between control and transitional plots. The multi-guild approach revealed sensitivity of forb diversity to *Solidago* invasion, in contrast to graminoids and bryophytes, for which no effects were observed

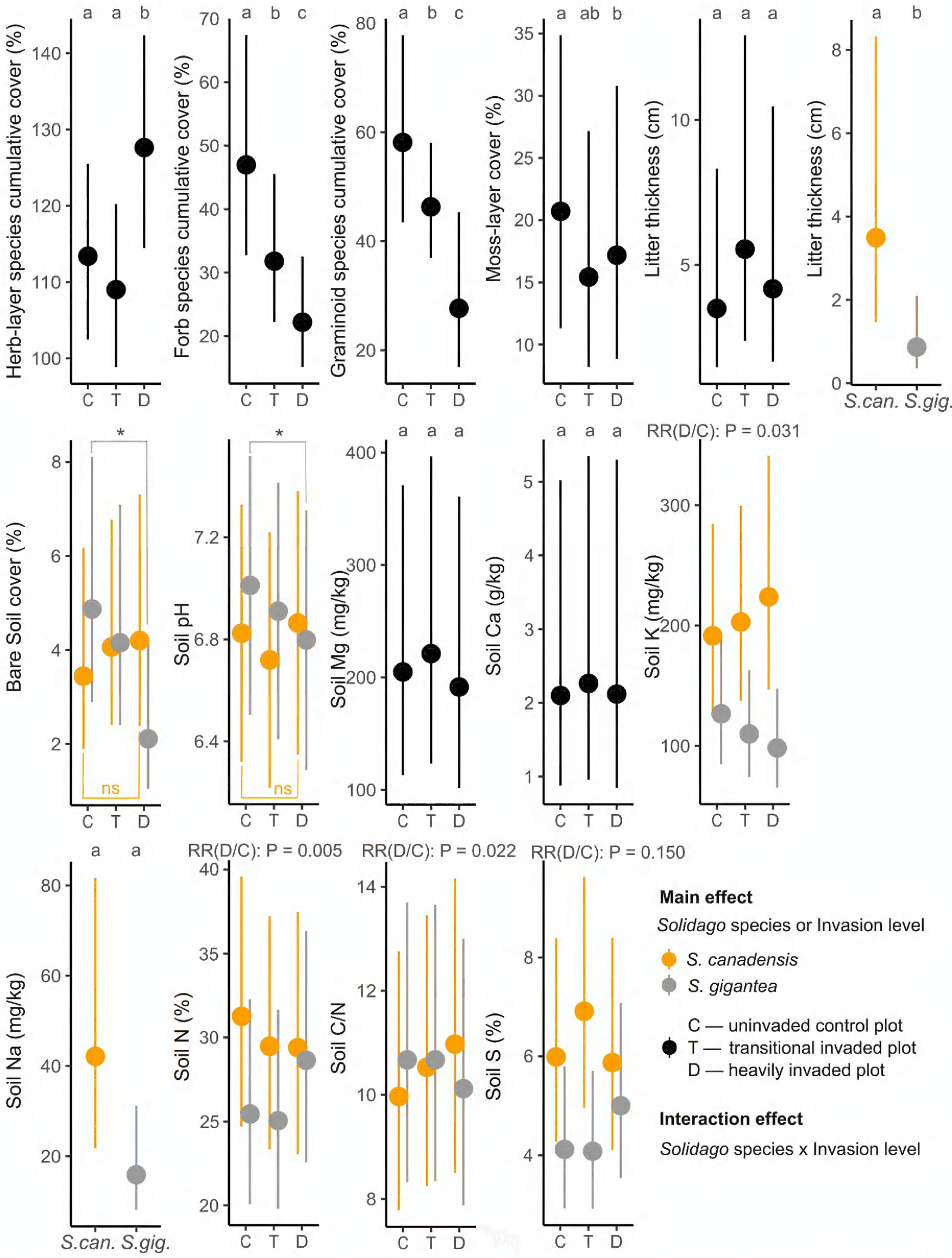

Figure 2. Comparison of the vegetation and soil chemical variables across invasion level (C – uninvaded control, T – transitional invaded, and D – heavily invaded plots; n = 60), based on significant effects in GLMMs and LMMs (Table 1). The circles represent predictions (model-based estimates) from (G)LMMs and error bars show their 95% confidence intervals. The interaction effect of *Solidago* species and invasion level is presented only when it is statistically significant in the model ($P < 0.05$); otherwise, the significant main effect is shown (significant differences indicated by different letters following results of Tukey-adjusted pairwise comparisons). A significant '*Solidago* species × invasion level' interaction was decomposed using within-species contrasts (D vs. C) and a contrast-in-contrast (difference-in-differences) test (RR/DC) comparing the invasion effect (D–C) between species.

Table 1. GLMMs and LMMs with the effects of explanatory variables on vegetation properties and soil chemistry (n = 60). Significant effects are in bold (parameter estimates for each effect are in Suppl. material 1: table S6). R^2 – marginal/conditional Nakagawa's pseudo-R^2.

Model term (df)	**Herb-layer species cumulative cover**			**Forb species cumulative cover**			**Graminoid species cumulative cover**		
	χ^2	P	R^2	χ^2	P	R^2	χ^2	P	R^2
Solidago (1)	7.460	**0.006**	0.38/0.49	0.659	0.417	0.32/0.59	0.295	0.587	0.44/0.50[XX]
Invasion level (2)	12.339	**0.002**		29.708	**<0.001**		31.220	**<0.001**	
Slope (1)	0.033	0.855		0.120	0.729		0.009	0.926	
Soil depth (1)	0.364	0.546		2.771	0.096		0.801	0.371	
Soil clay^2 (1/2)[X]	9.953	**0.007**		2.464	0.116		1.640	0.200	
Solidago × Inv. level (2)	1.267	0.531		0.531	0.767		1.659	0.436	
	Moss-layer cover			**Litter cover**			**Litter thickness**		
	χ^2	P	R	χ^2	P	R^2	χ^2	P	R^2
Solidago (1)	0.063	0.802	0.31/0.89	0.216	0.642	0.19/0.96	5.257	**0.022**	0.25/0.84
Invasion level (2)	9.389	**0.009**		1.820	0.403		6.384	**0.041**	
Slope (1)	0.236	0.627		0.822	0.365		0.162	0.688	
Soil depth (1)	0.519	0.471		2.244	0.134		0.020	0.889	
Soil clay (1)	5.902	**0.015**		1.690	0.194		4.298	**0.038**	
Solidago × Inv. level (2)	5.636	0.060		0.105	0.949		3.794	0.150	
	Bare soil cover			**Soil P**			**Soil pH**		
	χ^2	P	R^2	χ^2	P	R^2	χ^2	P	R^2
Solidago (1)	0.051	0.822	0.15/0.50	0.103	0.748	0.07/0.86	0.434	0.510	0.12/0.97
Invasion level (2)	2.324	0.313		1.656	0.437		6.707	**0.035**	
Slope (1)	0.227	0.634		0.516	0.473		4.173	**0.041**	
Soil depth (1)	0.476	0.490		2.213	0.137		11.442	**0.001**	
Soil clay (1)	1.078	0.299		0.349	0.555		2.032	0.154	
Solidago × Inv. level (2)	6.042	**0.049**		1.570	0.456		8.544	**0.014**	
	Soil Mg			**Soil Ca**			**Soil K**		
	χ^2	P	R^2	χ^2	P	R^2	χ^2	P	R^2
Solidago (1)	<0.001	1.000	0.66/0.92	0.307	0.580	0.54/0.94	3.152	**0.076**	0.61/0.93
Invasion level (2)	7.332	**0.026**		6.841	**0.033**		0.626	0.731	
Slope (1)	1.307	0.253		1.052	0.305		1.510	0.219	
Soil depth (1)	0.383	0.536		0.326	0.568		<0.001	0.990	
Soil clay (1)	45.205	**<0.001**		37.695	**<0.001**		21.136	**<0.001**	
Solidago × Inv. level (2)	2.988	0.224		4.560	0.102		6.345	**0.042**	
	Soil Na			**Soil C**			**Soil N**		
	χ^2	P	R^2	χ^2	P	R^2	χ^2	P	R^2
Solidago (1)	4.768	**0.029**	0.38/0.85	0.459	0.498	0.02/0.97	0.356	0.244	0.04/0.95
Invasion level (2)	4.119	0.128		4.540	0.103		7.605	**0.022**	
Slope (1)	0.389	0.360		2.417	0.120		0.014	0.907	
Soil depth (1)	0.528	0.467		0.022	0.882		0.073	0.787	
Soil clay (1)	3.586	0.058		0.295	0.587		0.017	0.897	
Solidago × Inv. level (2)	0.756	0.685		0.298	0.861		10.989	**0.004**	
	Soil C/N			**Soil S**					
	χ^2	P	R^2	χ^2	P	R^2			
Solidago (1)	0.075	0.784	0.06/0.95	3.530	0.060	0.17/0.85			
Invasion level (2)	1.103	0.675		2.505	0.286				
Slope (1)	3.474	0.062		0.522	0.470				
Soil depth (1)	0.063	0.802		1.622	0.203				
Soil clay (1)	2.241	0.134		0.826	0.363				
Solidago × Inv. level (2)	6.749	**0.034**		7.596	**0.022**				

[X]) For herb-layer cumulative cover, soil clay content was modelled using a second-order polynomial term to improve model fit/diagnostic (df = 2).
[XX]) The model included a plot-specific dispersion structure affecting Nakagawa R^2.

(Table 2, Fig. 3, Suppl. material 1: table S8). The lowest forb species richness was recorded in heavily invaded plots irrespective of *Solidago* species, while control and transitional plots did not differ significantly. A significant interaction effect of *Solidago* species and invasion level on Hill–Shannon and Hill–Simpson diversity indices of forbs showed an increasing trend of model predictions from control to heavily invaded plots at *S. canadensis* sites, and an opposite trend at *S. gigantea* sites (Fig. 3). Although pairwise contrasts among invasion levels within species were not statistically significant ($P > 0.05$), the magnitude of the invasion effect differed between the two invaders following the contrast-in-contrast test (the effect was stronger in case of *S. canadensis* – ratio = 0.56 and 0.50 for Hill–Shannon and Hill–Simpson, respectively). All models explained between 4–51% (marginal R^2) of the variance in the species diversity estimates, while the inclusion of random effects increased the explained variance to 20–81% (conditional R^2, Table 2). Sample-based rarefaction-extrapolation curves (gamma diversity) further showed a decrease in forb species richness with increasing invasion level in plots invaded by *S. gigantea*, whereas graminoids and bryophytes showed no such pattern. In contrast, in plots invaded by *S. canadensis*, none of the three plant guilds exhibited a decline in species richness along the invasion gradient (Suppl. material 1: fig. S2).

Table 2. GLMMs and LMMs with the effects of explanatory variables on species diversity estimates for the herb layer, forbs, graminoids and bryophytes (n = 60). Significant effects are in bold (parameter estimates for each effect are in Suppl. material 1: table S8). R^2 – marginal/conditional Nakagawa's pseudo-R^2.

Model term (df)	Hill–Species richness			Hill–Shannon index			Hill–Simpson index		
Herb layer	χ^2	P	R^2	χ^2	P	R^2	χ^2	P	R^2
Solidago (1)	0.039	0.844	0.33/0.72	0.041	0.839	0.43/0.71	0.283	0.595	0.51/0.63
Invasion level (2)	7.789	0.020		72.561	**<0.001**		76.317	**<0.001**	
Slope (1)	2.599	0.107		1.277	0.259		0.373	0.541	
Soil depth (1)	2.779	0.096		0.737	0.391		0.088	0.766	
Soil clay (1)	2.600	0.107		0.106	0.745		<0.001	0.986	
Solidago × Inv. level (2)	1.905	0.386		0.579	0.749		0.068	0.967	
Forbs									
Solidago (1)	0.332	0.564	0.38/0.75	1.112	0.292	0.23/0.81	0.632	0.426	0.16/0.74
Invasion level (2)	10.643	**0.005**		0.182	0.913		0.671	0.715	
Slope (1)	3.722	0.054		0.465	0.494		0.072	0.788	
Soil depth (1)	3.673	0.055		0.021	0.885		0.144	0.704	
Soil clay (1)	3.839	**0.050**		5.049	**0.025**		2.386	0.122	
Solidago × Inv. level (2)	1.999	0.368		8.709	**0.013**		10.121	**0.006**	
Graminoids									
Solidago (1)	1.318	0.251	0.04/0.26	0.315	0.575	0.09/0.61	0.418	0.518	0.10/0.52
Invasion level (2)	4.399	0.111		0.148	0.929		0.118	0.943	
Slope (1)	0.153	0.695		0.067	0.796		0.005	0.945	
Soil depth (1)	0.064	0.800		0.119	0.730		0.461	0.497	
Soil clay (1)	0.011	0.917		0.159	0.690		0.117	0.733	
Solidago × Inv. level (2)	0.994	0.608		2.539	0.281		2.808	0.246	
Bryophytes									
Solidago (1)	0.001	0.978	0.21/0.42	0.034	0.854	0.09/0.23	0.053	0.819	0.09/0.20
Invasion level (2)	4.142	0.126		3.113	0.211		2.852	0.240	
Slope (1)	4.673	**0.031**		0.039	0.843		<0.001	0.990	
Soil depth (1)	1.342	0.247		0.154	0.694		0.124	0.724	
Soil clay (1)	0.005	0.946		1.375	0.241		1.677	0.195	
Solidago × Inv. level (2)	1.672	0.433		0.498	0.780		0.650	0.723	

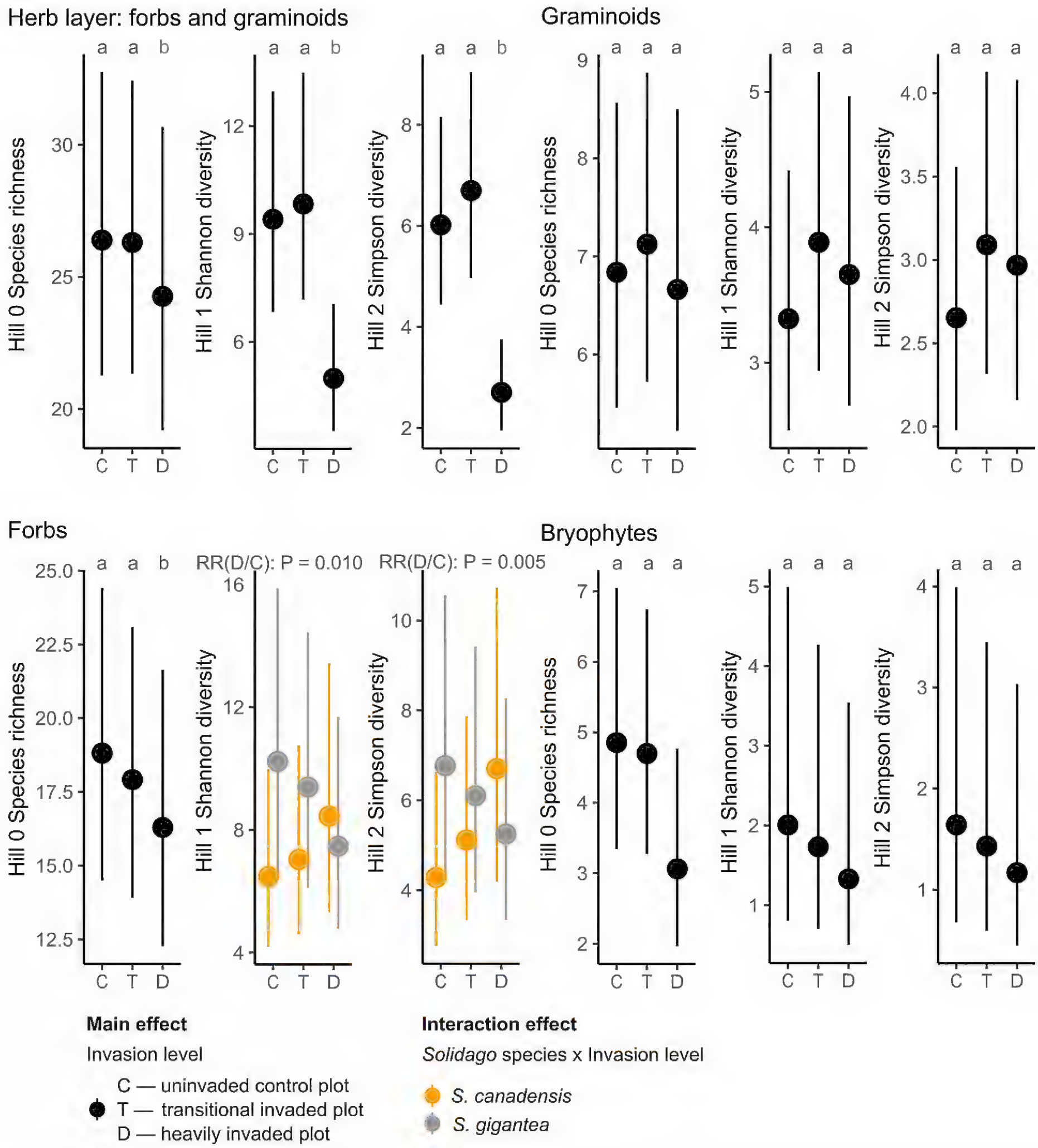

Figure 3. Comparison of species diversity of the herb layer, forbs, graminoids and bryophytes across invasion level (C – uninvaded control, T – transitional invaded, and D – heavily invaded plots; n = 60), based on significant effects in GLMMs and LMMs (Table 2). The circles represent predictions (model-based estimates) from (G)LMMs and error bars show their 95% confidence intervals. The interaction effect of *Solidago* species and invasion level is presented only when it is statistically significant in the model ($P < 0.05$); otherwise, the significant main effect is shown (significant differences indicated by different letters following results of Tukey-adjusted pairwise comparisons). A significant '*Solidago* species × invasion level' interaction was decomposed using within-species contrasts (D vs. C) and a contrast-in-contrast (difference-in-differences) test (RR/DC) comparing the invasion effect (D–C) between species. *Solidago* species were excluded from species richness and diversity estimates of forbs.

Species composition

The effect of invasion level on variation in species composition was significant throughout all tested plant guilds (herb-layer, forbs, graminoids), after accounting for environmental covariates and spatial structure (permutations restricted within

Table 3. Results of permutational multivariate analysis of variance (PERMANOVA) testing the effects of explanatory variables on herb-layer (forbs and graminoids) species composition based on Bray-Curtis dissimilarities. Marginal (Type III) tests are shown. Permutations (n = 999) were restricted within locality. R^2 values represent marginal (partial) effects of each term after accounting for all other variables in the model. Significant P-values (P < 0.05) are indicated in bold.

Predictor	DF	R^2	F	P
Solidago	1	0.035	2.469	0.749
Invasion level	2	0.019	0.682	**0.001**
Slope	1	0.031	2.156	0.155
Soil depth	1	0.052	3.693	0.141
Soil clay	1	0.057	4.040	0.163

locality). Its explanatory power was consistently low (marginal R^2 in a range of 0.018–0.019), yet contrasted with non-significant effect of *Solidago* species identity on compositional variation (Table 3, Suppl. material 1: tables S9–S10). These patterns were broadly consistent when forbs and graminoids were analysed separately. The full model for the herb-layer composition explained 24.8% of the total variation in Bray–Curtis dissimilarities (27.2% for forbs, 20.6% for graminoids). However, tests for homogeneity of multivariate dispersions indicated significant differences in within-group dispersion among invasion levels for herb-layer (F = 0.606, P = 0.002) and forbs (F = 0.965, P = 0.002), but not for graminoids (F = 0.053, P = 0.705). Species compositional heterogeneity increased with increasing invasion level, as indicated by mean distance to group centroid (C = 0.552; T = 0.539; D = 0.571).

NMDS ordination showed pronounced overlap in herb-layer species composition across invasion levels (Fig. 4), consistent with the low but statistically significant effect found by PERMANOVA (Table 3). Differences in group dispersion within the ordination reflected heterogeneity of multivariate variance among invasion levels. Indicator species analysis (IndVal) did not identify any characteristic species clearly differentiating invasion levels. Although six species showed preliminary associations with control plots (IndVal value > 0.5: *Agrimonia eupatoria*, *Daucus carota*, *Festuca rupicola*, *Leontodon hispidus*, *Ranunculus polyanthemos*, *Trifolium pratense*), none of these affinities remained significant after FDR correction (all P > 0.05). Similar compositional patterns indicating abundance shifts rather than species replacement (Suppl. material 1: table S7) were also recognized if species composition of forbs and graminoids were analysed separately.

Discussion

Our results highlight how incomplete assessments of invasion impact on plant species richness or diversity can be when only herb-layer (or total) values are considered. Grassland communities consist of various plant guilds (Diaz and Cabido 2001) that may differ in a range of functional traits (e.g. clonal growth strategy, rooting architecture, resource acquisition, shade tolerance) governing their capacity for competitive tolerance and their potential for spatial and temporal niche partitioning in the presence of plant invaders. We did not find consistent responses of plant guilds to plant invasions in semi-natural grasslands

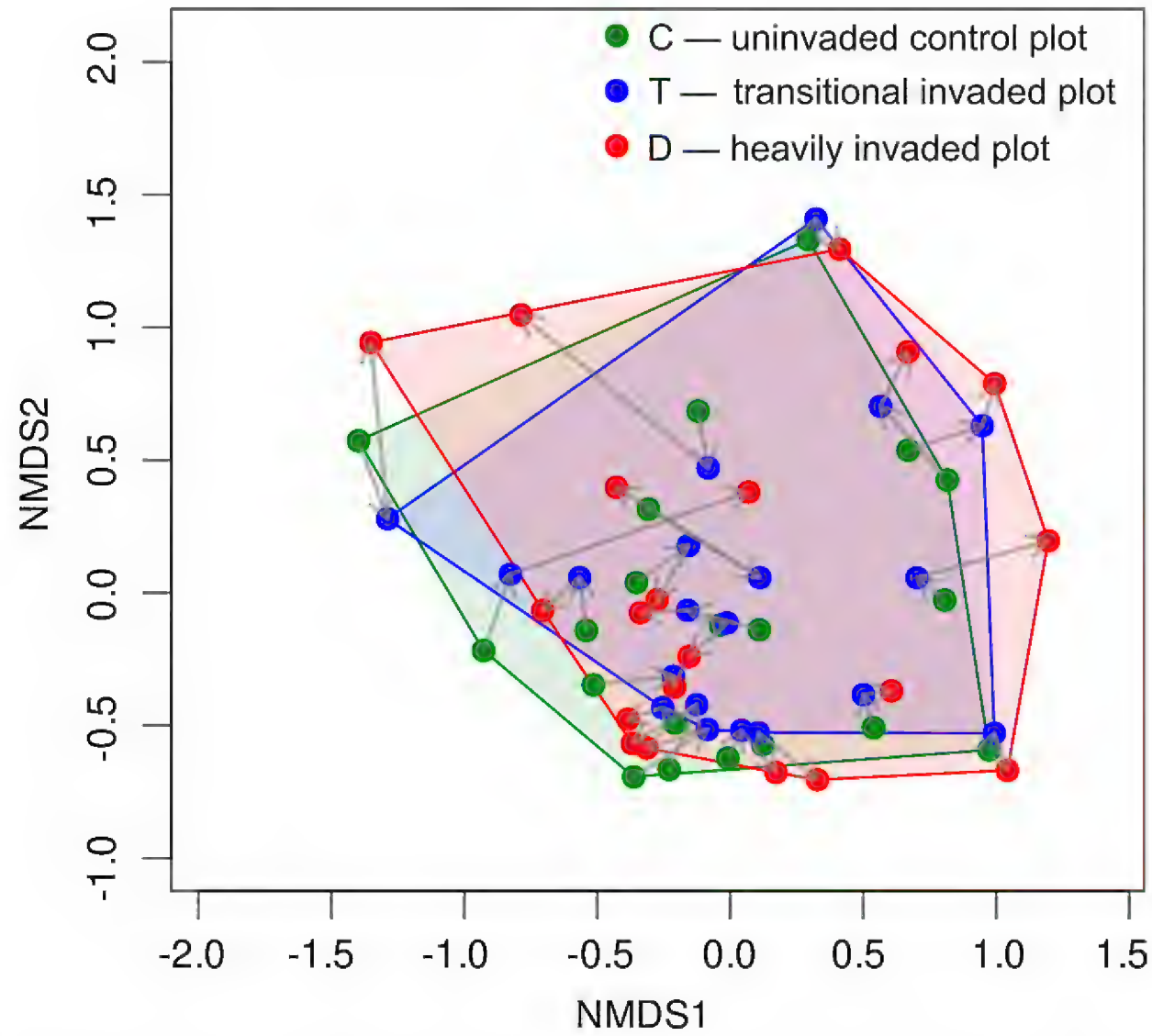

Figure 4. Non-metric multidimensional scaling (NMDS; k = 2, stress = 0.204) of Bray-Curtis dissimilarities in herb-layer (forbs and graminoids) species composition. Each point represents a sampled plot with colours indicating invasion level (C – uninvaded control, T – transitional invaded, and D – heavily invaded plots), and convex hulls indicate the extent of each group in ordination space. Arrows link plots of the same sampling site.

(hypothesis 1), as the invasive *Solidago* species reduced the species richness of forbs in heavily invaded plots, while having no invasion effect on graminoid and bryophyte diversity. Moreover, the response of forb Hill–Shannon and Hill–Simpson diversity to invasion level differed between the two *Solidago* species. These guild-specific responses illustrate their different susceptibility to invasion in semi-natural grassland communities. Our results also confirmed that both invasive species altered soil fertility properties (hypothesis 2), consistent with the recognised capacity of plant invaders to modify the soil environment (Ehrenfeld 2003; Liao et al. 2008). Although most of the observed variation in species diversity and ecological responses was explained by the shared invasive impact of both goldenrods – *Solidago* species identity being non-significant in most models – we also identified several species-specific effects.

Lower marginal R^2 (R^2m) than conditional R^2 values (R^2c) indicated that a substantial proportion of the variance was attributable to among-site differences captured by the random effect of site. The relatively similar R^2m and R^2c values observed for vegetation properties suggested that invasion level explained much of the variation independently of site effects. For herb-layer diversity, the high values of both R^2m and R^2c indicated that invasion intensity and local environmental conditions each contributed substantially to the observed patterns. In contrast, soil chemical properties showed pronounced discrepancies between R^2m and R^2c (e.g. soil pH: 0.12/0.97), reflecting site-level heterogeneity in soil conditions.

Species-specific invasion effect on the soil environment

Invasion by *S. gigantea* significantly affected soil pH and cover of bare soil, whereas effects on other soil variables (N, C/N ratio, K) and litter thickness differed between both goldenrods. Specifically, a decrease of soil pH in plots invaded by *S. gigantea* could be explained by its release of acidic compounds (Weber and Jakobs 2005). The lower pH values in the invaded plots were consistent with the belowground effects of this species reported in grasslands (e.g. Quist et al. 2014). However, direct eco-physiological constraints induced by the decline of soil pH on plant species performance and consequently on diversity values are unlikely, as most of the study sites were situated on productive soils. The acidifying effect of *S. gigantea* could instead play a role on resource-poor and acidic sites, where it may accelerate the release of some phytotoxic metal ions. We suppose that the acidifying effect observed in our study system was restrained by calcium carbonate, which increases soil buffering capacity mainly on calcareous soils (Chapuis-Lardy et al. 2006). This is probably also why we did not detect the often reported belowground effect of invasive *S. gigantea* on phosphorus concentration (Herr et al. 2007).

Our results showed that an increase of soil N content was accompanied by a decline of soil C/N ratio in plots heavily invaded by *S. gigantea*. This pattern likely reflects the habitat engineering capacity of this invasive species, which may be particularly pronounced on recorded sandy soils. Individuals of *S. gigantea* produce long and branching rhizomes able to fill space in the topsoil layers, and invest resources to clonal growth forming dense polycormons (Schmid et al. 1988; Szymura and Szymura 2015; Skokanová 2023; Roscher 2025). Although goldenrods are a high nitrogen-uptake invasive plant (Zhang et al. 2009a), much of the assimilated nitrogen can be returned to the soil through decomposition of aboveground biomass (Liao et al. 2008). In our case, *S. gigantea* formed a topsoil litter layer and reduced a bare soil cover in an otherwise organically poorer soil. These structural changes, critical to carbon and nitrogen cycling processes, are reinforced by the effect of *S. gigantea* on the composition and functioning of soil microbial community (Scharfy et al. 2010), which facilitates litter decomposition and net nitrogen mineralization. Moreover, faster decomposition rate of *S. gigantea* litter compared to native graminoids (Goossens et al. 2025) could therefore promote rapid nitrogen release and accumulation in soils of invaded plots, mainly as vegetation in control plots was often composed of native grasses. In addition to nitrogen dynamics, increased carbon mineralisation reported from *S. gigantea* invaded systems (e.g. Koutika et al. 2007) may reduce soil carbon stocks over time, thereby contributing to the decline in the soil C/N ratio observed in heavily invaded plots. This pattern contrasted with the decline in soil N content and the increase in soil C/N ratio recognized in plots invaded by *S. canadensis*. This species was frequently recorded on clay-rich soils with a relatively high pre-existing organic matter, where its impact on the C/N ratio may be greater. We hypothesise that the carbon inputs derived from the litter layer, and potentially augmented by carbon-based allelochemicals released from *S. canadensis* roots (Zhang et al. 2011; Yuan et al. 2013), exceeded the rates of nitrogen mineralization. This stoichiometric imbalance could favour the partial immobilisation of nitrogen within the soil microbial biomass at the expense of net mineralization (Wang et al. 2023).

The contrasting trends in soil K content between sites dominated by *S. gigantea* and *S. canadensis* most likely reflect an interplay between pre-invasion

soil fertility and species-specific life strategies. The decline in exchangeable soil K in plots invaded by *S. gigantea* corresponded to the conservative nutrient-use strategy of this species (Scharfy et al. 2009), which probably tended to immobilise available nutrients in its extensive belowground biomass rather than returning them rapidly to the soil. Unlike nitrogen, K released from decomposing biomass does not form stable organic compounds but remains in soluble or exchangeable forms. Consequently, it is prone to leaching losses, particularly in sandy soils with low cation exchange capacity, which may further exacerbate K depletion in invaded plots. On the other hand, the higher cation exchange capacity of clay-rich than sandy substrates may support soil K retention under *S. canadensis* invasion, where accelerated nutrient cycling through litter decomposition and enhanced microbial activity could progressively enrich the exchangeable K pool in the soil.

Invasion impact on the species diversity of plant guilds

The role of dominant plant species is often invoked to explain community assembly patterns. It is widely accepted that high contributions to community biomass and interspecific competition of dominant species will reduce the diversity of plant species on a site (Gioria and Osborne 2014; Hejda et al. 2021). In our study, goldenrod invasions led to an increase of cumulative herb-layer cover. Both invasive species *S. canadensis* and *S. gigantea* likely altered species competitive hierarchies within the herb-layer, which was accompanied by a decline in herb-layer richness and diversity indices in heavily invaded plots. The observed accumulation of litter produced by goldenrods may have further reinforced these competitive effects by limiting light penetration and reducing bare-soil microsites suitable for seed germination.

However, this general pattern masked a functionally selective invasion impact across plant guilds. While forb assemblages experienced both richness losses in heavily invaded plots and invader-specific contrasts in diversity responses, graminoid richness and diversity remained largely resistant to invasion pressure. These plant guilds differ in their capacity to uptake and utilise mineral nutrients and in their tolerance to competitive and stressful environments (You et al. 2017; Grange et al. 2023; Zhang et al. 2023). Many of the recorded forb species were light-demanding and particularly sensitive to canopy closure and litter accumulation imposed by invasive goldenrods. In contrast, the most common graminoids (e.g. *Arrhenatherum elatius*, *Dactylis glomerata*, *Elytrigia repens*, *Festuca rupicola*) possess traits (e.g. narrow vertical leaves, clonal growth, extensive fibrous root system) that enable them to maintain growth and efficiently utilise resources under invasion pressure (e.g. Fenesi et al. 2015). Graminoids also tend to tolerate litter accumulation better than many forbs and may rely on vegetation propagation, which allows them to colonise small patches within the dense herb-layer, and reduces their dependence on seedling recruitment. Although the invasive species strongly reduced cumulative graminoid cover, they did not fully outcompete these species, which is consistent with the absence of invasion effect on graminoid diversity measures. Species composition patterns also suggested that invasions did not establish distinctive plant assemblages, but rather triggered community reorganization driven primarily by gradual shifts in abundance and dominance, accompanied by species turnover within the existing species pool.

The greater vulnerability of forbs than graminoids to invasion pressure may be further attributed to the higher susceptibility of forbs to allelopathic compounds produced by the dense and vigorous rhizome systems of both goldenrod species (Güsewell et al. 2006; Schlaepfer et al. 2010). Allelopathy has already been shown to importantly modify the interactions of other plants with soil mycorrhizae (Abhilasha et al. 2008; Yuan et al. 2013), with a more pronounced effect on forbs than on graminoids (Grange et al. 2023). This could be addressed to a lower pre-invasion mycorrhizal dependency in graminoids (Grange et al. 2023), and their overall higher phytotoxic tolerance (Zhang et al. 2023).

Both goldenrods induced divergent trends in Shannon and Simpson diversity indices for forb species. While forb diversity tended to increase from control to heavily invaded plots in stands dominated by *S. canadensis*, the opposite pattern was observed for *S. gigantea*. These contrasting responses of diversity estimates were attributable to shifts in community evenness (Hejda et al. 2021) rather than consistent changes in species richness. Such differences could partly arise from species-specific effects of the invaders on soil processes and site productivity. In particular, the increased nitrogen availability and reduced C/N ratio associated with *S. gigantea* plots suggested accelerated nutrient cycling and enhanced productivity, which can in turn intensify light competition (Dybzinski and Tilman 2007) and favour dominance of a limited number of competitively superior species. On the other hand, the higher C/N ratio and decline of nitrogen availability recorded in *S. canadensis* stands may indicate greater carbon inputs and partial nitrogen immobilisation within the soil microbial biomass (Wang et al. 2023). This could potentially mitigate competitive asymmetry and thereby facilitate the persistence of a large number of subordinate forb species in invaded communities.

Sample-based rarefaction curves indicated the reduction in forb diversity associated with *S. gigantea* invasions at the landscape level (gamma diversity). Because forbs represented the most species-rich functional group in the studied grasslands, this pattern suggests that *S. gigantea* invasion may contribute to a decline in plant diversity at the landscape scale. Local plant communities dominated by resource-acquisitive species (in our case invaded plots) may modify community-environment relationships, but they usually tend to have low ecosystem resistance (Nagy et al. 2020). These patterns highlight the importance of management actions aimed at limiting invasive species dominance and promoting the recovery of native plant assemblages (Świerszcz et al. 2024).

Moss-layer cover decreased in heavily invaded plots. The mechanism responsible for this pattern extends beyond direct aboveground biomass competition induced by tall canopy-forming *Solidago* species or physical suppression by litter (van der Wal et al. 2005), as moss-layer cover did not correlate with cumulative herb-layer cover and litter metrics (thickness and cover). Instead, the decline likely reflected the combined roles of pre-existing soil texture and goldenrod invasion. Although the underlying mechanisms cannot be fully disentangled from our data, soil clay content emerged as a significant covariable, suggesting an independent effect of soil texture on moss-layer cover that should be accounted for when evaluating invasion impacts. Soil texture regulates moisture dynamics critical for poikilohydric bryophytes, and this effect may be further mediated by stand-level microclimatic changes (e.g. altered humidity and vapour pressure deficit) due to dense goldenrod stands. Clay-rich soils have generally higher P retention capacity, which may suppress moss-layer development under elevated P availability

(indicated by a weak negative correlation between soil P and moss-layer cover) through either direct eco-physiological constraints (Arróniz-Crespo et al. 2008) or indirect facilitation of herb-layer competitors. Together, these factors appear to act as generalized constraints on overall moss-layer cover rather than species-selective filters restructuring bryophyte community assembly, as no measures of bryophyte species diversity changed along the invasion gradient.

Limitations of our study

A spatial invasion-gradient approach is used to infer invasion dynamics and impacts when long-term historical data are unavailable. However, such gradients may be confounded by underlying environmental heterogeneity, management history, or non-equilibrium processes, meaning that their reliability depends on careful modelling and appropriate covariate control (Stricker et al. 2015; Tisseuil et al. 2016; Ibáñez et al. 2023). In our study, the impact of *Solidago* species was studied at sites with well-established, self-reproducing populations of the two invasive species present for at least five years, but the precise residence time of invasion was incomplete at some sampling sites. Therefore, differences in *Solidago* cover among adjacent plots were used as a proxy for invasion intensity. Relatively weak soil responses do not necessarily indicate recent invasion, because changes in soil chemical properties may develop gradually and depend on local soil conditions and plant-soil feedback processes (Dassonville et al. 2008; Vilà et al. 2011; Dostál et al. 2013; D'Antonio and Flory 2017; Oduor et al. 2022; Thakur et al. 2025). Our snapshot sampling may also have underrepresented vernal species whose aboveground biomass persists only briefly outside the phenological optimum of goldenrod species. However, vernal species were expected to contribute little to overall community structure due to the short duration of their aboveground presence compared with the dominant canopy of goldenrods.

Conclusions

Species diversity of plant guilds responded differently to ecological constraints imposed by invasive goldenrods, highlighting the limitations of evaluating invasion impacts using only total herb-layer diversity. Species richness of forb assemblages declined in heavily invaded plots, likely reflecting intensified competition and litter accumulation generated by dense *Solidago* stands, whereas bryophyte and graminoid diversity showed no change across invasion levels. Graminoids appeared more tolerant of the competitive and stressful conditions in invaded plots than forbs. In our study system, most variation in diversity patterns was associated with the effects of *Solidago* invasion overall, although several species-specific impacts also emerged, including contrasting effects of *S. gigantea* and *S. canadensis* on forb diversity indices and soil chemistry. A complementary assessment of *Solidago* invasion effects across plant guilds and ecosystem components thus allows for a better understanding of mechanisms underlying plant invasion in semi-natural grasslands.

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Supplementary material 1

Supplementary information

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Data type: zip

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

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Artificial Intelligence (AI) use

The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI.
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Author contributions

MS – Data curation, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing, BJ – Data curation, Formal analysis, Methodology, Visualization, Writing – original draft, Writing – review & editing, BŠ – Conceptualization, Methodology, Investigation, Writing – original draft, Writing – review & editing, SŠ – Investigation, Writing – review & editing, RH – Funding acquisition, Investigation, Project administration, Writing – review & editing, JM – Data curation, Investigation, Writing – review & editing, EG – Investigation, Writing – review & editing, PŠ – Investigation, Writing – review & editing, IH – Investigation, Writing – review & editing, PM – Investigation, Writing – review & editing, DG – Investigation, Writing – review & editing, MJ – Investigation, Writing – review & editing, JK – Investigation, Writing – review & editing, KS – Conceptualization, Data curation, Investigation, Methodology, Supervision, Writing – original draft, Writing – review & editing.

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Data availability

Data associated with the results of statistical analyses and species composition of sampling plots (vegetation relevés) are available in Supplementary Information.